

Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest

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Summary We used 20-mm-long, Granier-type sensors to quantify the effects of tree size, azimuth and radial position in the xylem on the spatial variability in xylem sap flux in 64-year-old trees of *Taxodium distichum* L. Rich. growing in a flooded forest. This information was used to scale flux to the stand level to investigate variations in half-hourly and daily (24-hour) sums of sap flow, transpiration per unit of leaf area, and stand transpiration in relation to vapor pressure deficit (D) and photosynthetically active radiation (Q_o). Measurements of xylem sap flux density (J_s) indicated that: (1) J_s in small diameter trees was 0.70 of that in medium and large diameter trees, but the relationship between stem diameter as a continuous variable and J_s was not significant; (2) J_s at 20–40 mm depth in the xylem was 0.40 of that at 0–20 mm depth; and (3) J_s on the north side of trees was 0.64 of that in directions 120° from the north. Daily transpiration was linearly related to daily daytime mean D , and reached a modest value of 1.3 mm day⁻¹, reflecting the low leaf area index (LAI = 2.2) of the stand. Because there was no soil water limitation, half-hourly water uptake was nearly linearly related to D at $D < 0.6$ kPa during both night and day, increasing to saturation during daytime at higher values of D . The positive effect of Q_o on J_s was significant, but relatively minor. Thus, a second-order polynomial with D explained 94% of the variation in J_s and transpiration. An approximately 40% reduction in LAI by a hurricane resulted in decreases of about 18% in J_s and stand transpiration, indicating partial stomatal compensation.

Keywords: cypress swamp, hurricane effect, scaling, transpiration, xylem sap flux.

Introduction

Xylem sap flux density (J_s) of trees is used both to estimate stand transpiration (E_C) based on a variety of scaling approaches (Köstner et al. 1992, Granier and Loustau 1994, Granier et al. 1996, Oren et al. 1996, 1998a, Martin et al. 1997), and to investigate environmental effects on temporal variation in transpiration rate per unit of leaf area (E_l). Parameter E_l is calculated by multiplying J_s by sapwood-to-leaf area ratio ($A_S:A_l$), or dividing whole-tree transpiration by its esti-

mated leaf area (Martin et al. 1997, Oren et al. 1998a, Phillips and Oren 1998). The assumption implicit in the calculation of both E_C and E_l is that all contributors to systematic variations in J_s are represented (Oren et al. 1998b). Also implicit in the calculation of E_l is that it is directly related to J_s measured in the lower stem; i.e., the quantity of water discharged from storage in the plant into the transpiration stream in the morning is small relative to uptake, and the quantity recharged by uptake later in the day is small relative to transpiration.

Sap flux measured in the xylem with Granier-type sensors represents the flux averaged over the sensor length (typically 20 mm)—a relatively small area in the xylem. Because it is not generally possible to link a particular portion of xylem to the specific area of foliage supported by it, a weighted mean flux per unit of hydroactive xylem area (i.e., sapwood) must be estimated and related to the mean leaf area per unit of sapwood area. At the individual tree level, mean flux can be obtained with a sufficient number of sensors in each tree (cf. Olbrich 1991), and an accurate estimate of tree leaf area can be obtained with detailed measurements within the crown (Waring et al. 1982, Oren et al. 1986). However, the more common approach, designed to scale flux measurements to stand level water use, relies on obtaining mean flux and a mean leaf-to-sapwood area ratio at the population level (Oren et al. 1998b).

Estimating weighted mean J_s in a stand requires that potential systematic variations in flux are assessed, including variations in J_s with depth (Granier et al. 1994, see review in Phillips et al. 1996), azimuth (Daum 1967, Ěermák et al. 1984, Fichtner and Schulze 1990), tree size (Martin et al. 1997), and degree of competition (Oren et al. 1998b). Sap flux can then be scaled by using the amount of xylem representing each distinct flux class (Oren et al. 1998b).

The other variable necessary to estimate E_l is sapwood-to-leaf area ratio ($A_S:A_l$). This variable also changes systematically, decreasing with increasing distance between the sensor height and base of crown (Waring et al. 1982), with increasing evaporative demand (Oren et al. 1986, Mencuccini and Grace 1995), and with decreasing growth rate, which reduces hydraulic conductance (see Margolis et al. 1995). If weighted mean J_s is estimated at the stand level at a daily time step, then a population-level estimate of $A_S:A_l$ can be used to calculate

daily E_1 and evaluate its responses to daily variation in the environment, thereby avoiding the effect of stored water on transpiration (e.g., Oren et al. 1996, Martin et al. 1997). However, during the day, sap flow at the base of trees may be decoupled from transpiration as a result of water storage in tissues above the sensor position (Ěermák et al. 1980, Schulze et al. 1985, Loustau et al. 1996), obscuring the quantitative link between environmental driving variables and transpiration. Thus, analyses of E_1 responses to the large variations in environmental conditions at sub-daily (e.g., half-hourly) time scales require an explicit treatment of the lag between water uptake and transpiration (Phillips and Oren 1998).

At sub-daily time scales, capacitance has been accounted for through measurements or modeling with various degrees of success (Hunt et al. 1991, Holbrook 1995, Loustau et al. 1996, Phillips et al. 1997); however, variations in capacitance are most often partially circumvented by simply lagging the time series of J_S to match that of D (visually or through cross-correlation analysis; Granier and Loustau 1994, Hinckley et al. 1994, Bernhofer et al. 1996, Martin et al. 1997, Phillips and Oren 1998). Until methods for quantifying the relationship between stored water and transpiration are available, it is best to select conditions in which stored water has little effect on transpiration. For example, some species have a greater capacity for storage than others (see Holbrook 1995); small trees have a relatively small capacity for water storage (Carlson and Lynn 1991, Pataki et al. 1998a); and as soil dries, water from storage contributes a greater proportion of the daily flux (Phillips et al. 1996). The supply of water to transpiration from capacitance is lowest at intermediate water potentials, past the point of capillary water release, and before the point of cavitation water release (Edwards and Jarvis 1982, Tyree and Yang 1990).

Simplifications are often used in field studies to eliminate variability in resistance to flow in one part of the transpiration pathway, thus providing greater confidence in interpreting the variability in the remaining pathway. For example, it is assumed that soil and soil-root interface resistances are relatively small and constant under moist soil conditions, and thus variation in stomatal conductance can be evaluated in relation to variability in photosynthetically active radiation (Q_0) and vapor pressure deficit (D ; Cienciala and Lindroth 1995, Granier and Bréda 1996). However, even in homogeneous, moist soils, spatial variation in water availability and rooting distribution can be large (Katul et al. 1997), and resistance to water movement in the rhizosphere increases daily in direct relation to the transpiration rate as water is depleted near roots (Kramer 1983, Aylmore 1993). Flooded stands composed of flood-tolerant species are more suitable for such an investigation because the effects of spatial and temporal variations in water availability on J_S (Hatton and Vertessy 1990) are largely eliminated under flooding.

We investigated potential contributors (tree size, azimuth, and radial position within the xylem) to systematic variations in J_S in a 64-year-old stand of *Taxodium distichum* L. Rich. growing under nearly continuous flooding with flowing, cool water in an impoundment formed artificially before planting, and maintained since by beaver activity. These conditions

largely eliminated the effects of diurnal and daily moisture variations in the rhizosphere of large trees, so that the effects of variations in atmospheric conditions on sap-flux-scaled E_1 can be isolated. The experimental design allowed us to quantify the effects of D in the canopy zone, and the effects of Q_0 above the canopy, on transpiration under conditions of constant, near zero soil water potential.

Taxodium distichum is a highly flood-tolerant species (Megonigal et al. 1997, Hall and Harcombe 1998), particularly under conditions when floodwaters are flowing (Brown and Montz 1986, Pezeshki and Anderson 1997). Conductance in *T. distichum* seedlings nearly or completely recovers to pre-flooding values after two weeks of transient response (Pezeshki et al. 1995, Allen et al. 1996), in part because of the production of adventitious roots (Hook 1984, Megonigal and Day 1992, Pezeshki and Anderson 1997). The physiology of mature *T. distichum* has rarely been studied (but see Brown 1981), but it is known that artificial flooding of mature individuals results in the production of water roots within 3 years following flooding (Harms et al. 1980). Thus, both species and site conditions are optimal for investigating the effects of variation in atmospheric conditions on sap-flux-scaled transpiration. We also took advantage of an unplanned experiment in leaf area reduction, performed by a hurricane, to evaluate the effect of leaf-area reduction on transpiration.

Materials and methods

The study was conducted at the Lost Shoe Swamp, Duke Forest, Durham, North Carolina (35°52' N, 79°59' W), where mean annual temperature is 15.5 °C, and mean annual precipitation is 1140 mm. Seedlings of *T. distichum* were planted in 1933 by C.F. Korstian in an artificial impoundment formed specifically for this stand by dikes at an elevation of about 130 m above sea level. The site is flooded almost continuously to about 0.5 m by slowly flowing water. *Fraxinus pennsylvanica* Marsh. became established as a minor component in the stand during dry years in which the soil surface was not inundated. The *F. pennsylvanica* trees are restricted to the lower canopy, many are dead, and the rest display irregularly shaped, small crowns supporting few leaves. Small individuals of *T. distichum* are healthy and support a normal crown. At age 64, tree diameter at 1.3 m aboveground ranged from 188 to 557 mm, reaching a height of about 27 m. Crown base of small individuals reached about 2 m above soil surface. Although the stand has high basal area, and relatively high sapwood area (Table 1), its leaf area index (LAI; estimated with the Canopy Area Analyzer, LAI2000, Li-Cor, Inc., Lincoln, NE) was low, producing a ratio of 0.07 m² leaf area per cm² breast height sapwood area (and its inverse, $A_S:A_1 = 0.0014 \text{ m}^2 \text{ m}^{-2}$), reflecting the large distance to the crown base.

The study was performed in two phases. In Phase 1, on October 1, 1995, data were collected to assess effects of radial and azimuth positioning of sap flow sensors and tree size on J_S . In Phase 2, on August 22–27, 1996, data were collected to evaluate the effects of D and Q_0 on J_S . On September 8–14, we made measurements to test the hypothesis that the J_S behavior quantified in August was not altered by a considerable stand-

Table 1. Stand characteristics.

Quantity	<i>T. distichum</i>	<i>F. pennsylvanica</i>
Stand density (N ha ⁻¹)	722	56
Quadratic DBH (mm)	360	312
A _B :A _G (m ² ha ⁻¹)	73.6	4.3
A _S :A _G (m ² ha ⁻¹)	31.7	–
LAI	2.2	–

wide defoliation caused by hurricane Fran on September 5 (sustained winds of 35 m s⁻¹). During both phases, *T. distichum* leaves did not show signs of autumn senescence. Although 1996 was dry relative to the mean until the hurricane deposited more than 100 mm of rain in 48 h, the soil in the study area was inundated during the entire study period in both years.

In Phase 1, the diameters at breast height of trees within a 15 m radius from the center of the stand were measured, and trees were classified into three groups, each representing a third of the size range in tree basal area. Then, 12 trees per group were randomly assigned to each of three azimuth directions, 120° apart: north, southeast and southwest. This assignment resulted in an uneven distribution of trees among the three size categories (Table 2). There was no difference among azimuth directions in the mean diameter of trees assigned to each size class ($P > 0.05$, one-way ANOVA). The selected 36 trees were equipped for sap flux measurement.

Sap flux densities were measured with Granier-type sensors. Each sensor is composed of a heated (constant heat flow) and unheated thermocouple pair, connected in opposition to measure temperature difference, as described by Granier (1987). The 20-mm-long sensors were installed in the outer xylem band at 1.3 m above the soil surface in 36 trees. In the 12 trees measured towards the north, Granier-Phillips-type sensors, a modified Granier-type sensor construction based on Phillips et al. (1996), were used to measure sap flow separately in the outer 20 mm xylem and the next 20 mm band of xylem (20–40 mm from the cambium, hereafter termed “inner xy-

Table 2. Number (*n*) and mean diameter at 1.3 m aboveground (1 SE) of sampled *Taxodium distichum* trees for each size class in each of the three measurement aspects. Groups represented by different letters are different ($P < 0.05$).

Sensor aspect	Size class	<i>n</i>	Diameter (mm)
North	Small	4	238 (17) a
	Medium	4	400 (14) b
	Large	4	474 (31) c
Southwest	Small	6	240 (9) a
	Medium	3	378 (4) b
	Large	3	523 (12) c
Southeast	Small	5	241 (8) a
	Medium	3	413 (17) b
	Large	4	498 (30) c

lem”), using one unheated reference thermocouple in the xylem 10–30 mm from the cambium. Sap flux density (J_s , g H₂O m⁻² sapwood s⁻¹) was calculated from the temperature difference, relative to the maximum difference which occurs at times of zero flow. Complete information on sensor installation and flux calculations can be found in Granier (1987) and Phillips et al. (1996). This phase of the study, designed primarily to evaluate the effects of azimuth, depth in the xylem, and tree size on J_s , was performed within one day because of the large power requirements of 48 sensors (the site does not have a power line).

In Phase 2, sample size was reduced to 10 trees measured only towards the north, five trees were equipped with Granier-Phillips-type sensors and the remaining five with standard Granier-type sensors. The trees ranged in diameter from 229 to 557 mm. One knee was also measured to quantify the potential error-causing thermal gradients under conditions of no flux; there was no diurnal pattern of temperature differences between the heated and unheated probes in the knee, indicating the absence of a thermal gradient.

To calculate D (kPa), air relative humidity and temperature were measured (Vaisala HMP 35C, Vaisala, Inc., Finland) at a height corresponding to two thirds of the canopy length from the canopy base. In addition, in Phase 2, Q_o (μmol m⁻² s⁻¹) was measured above the canopy by attaching a Li-Cor LI-190S sensor to the end of a telescopic pole, extending the pole above the canopy, and attaching it to the stem within the crown of a tree. Values of Q_o are available only for the pre-hurricane period, because the sensor was damaged in the storm. All xylem flux and micrometeorological sensors were sampled with a multichannel data logger (Delta-T Devices, Ltd., Cambridge, U.K.) at 30-s intervals, and 30-min means were recorded. Logger and power-control boxes were stored in a plastic trunk, positioned on a wooden platform, about 1 m above the soil surface, and 0.5 m above the water level before the hurricane.

The thickness of the hydroactive xylem, used to estimate plot-level sapwood area in each band, was obtained from increment cores taken from the 10 trees monitored for xylem flux in the second phase, which were representative of the range in tree size in the plot. There was no relationship between tree diameter and (1) number of growth rings in the outer xylem ($P > 0.2$), or (2) number of rings in the sapwood ($P > 0.2$), or (3) sapwood depth ($P = 0.08$, $r^2 = 0.25$), and thus a mean depth of 47.5 mm (SE = 4.6 mm) was used for scaling, on the assumption that J_s beyond 40 mm depth is similar to that in the 20–40 mm band. Given the reduced flux with depth in the xylem, this may represent a slight overestimation in stand-level transpiration.

All statistical analyses were performed with the SAS software package (SAS Institute, Cary, NC). Three-dimensional analysis was performed by stepwise multiple regression with an $\alpha = 0.05$ for tolerance.

Results

In Phase 1, variability in J_s was used to calculate the number of samples required to bring the coefficient of variation to

within 15% in each sampled category. The number ranged from seven sensors for the southeast side of trees, to 10 sensors for small trees. On October 1, 1995, daily J_S at the northerly sensor was 0.64 of that of the mean J_S at the two sets of southerly sensors, both of which recorded similar flux (Figure 1A; one-way ANOVA, $P < 0.01$, Tukey's t -test among the means using $P < 0.05$). Values of J_S in inner and outer xylem on the north side were similar (Figure 1A; Student's t -test, $P > 0.15$); and the outer J_S of small trees (Table 2) was 0.70 of that of medium and large trees (Figure 1B; $P < 0.01$). However, there was no direct relationship between tree diameter and J_S ($P > 0.2$). A two-way ANOVA for unbalanced design and uneven replication detected no interaction effect on J_S between sensor direction and tree size ($P > 0.2$). Over the day, J_S in all directions and at both depths in the xylem decreased as D stabilized in the early afternoon, but increased slightly and temporarily when D rose sharply (Figure 2). Because differences in J_S shown in Figure 1 originated from differences in midday flux, and not as a result of lags among the half-hourly J_S patterns in response to azimuth, size, or depth, the time series of all categories were highly correlated with each other at zero lag (minimum $r^2 = 0.98$).

In Phase 2, designed to evaluate the relationships between J_S and Q_o and D , daily J_S in the inner xylem averaged 0.40 of that at the outer sensors on the north side of trees (Figure 3A). There is no apparent explanation for the inconsistency of results in the radial trend between Phases 1 and 2, except that fluxes were lower on October 1, 1995 ($J_S < 10 \text{ g m}^{-2} \text{ s}^{-1}$ on the north side) than on August 22–27, 1996. In Phase 2, differences in J_S between outer and inner xylem were also difficult to detect under conditions of low flux (e.g., September 11, 1996). Differences in J_S between outer and inner xylem, were maintained during most of the daylight period, were highest at midday, and lowest on days of low D . Ten days after the study was terminated, but before the instruments were retrieved from the site, hurricane Fran passed over the region (Wurman and Winslow 1998), stripping a large quantity of foliage from the *T. distichum* trees, although no trees were broken or uprooted in the plot. This unplanned defoliation allowed us to test the

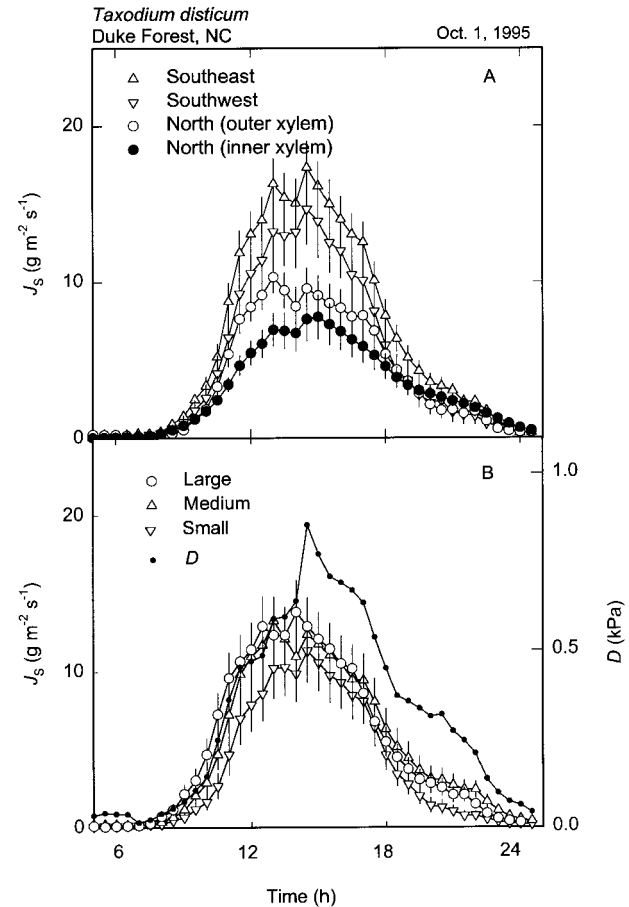


Figure 2. Half-hourly patterns of sap flux density (J_S) in (A) three azimuth categories and two depth categories, and (B) three tree size classes. Vapor pressure deficit (D) is also shown. Vertical lines represent ± 1 SE (see Table 1 for values of n).

hypothesis (based on the findings of Pataki et al. 1998b) that defoliation results in an increase in flux per unit of leaf area to compensate for the reduction in leaf area, resulting in an

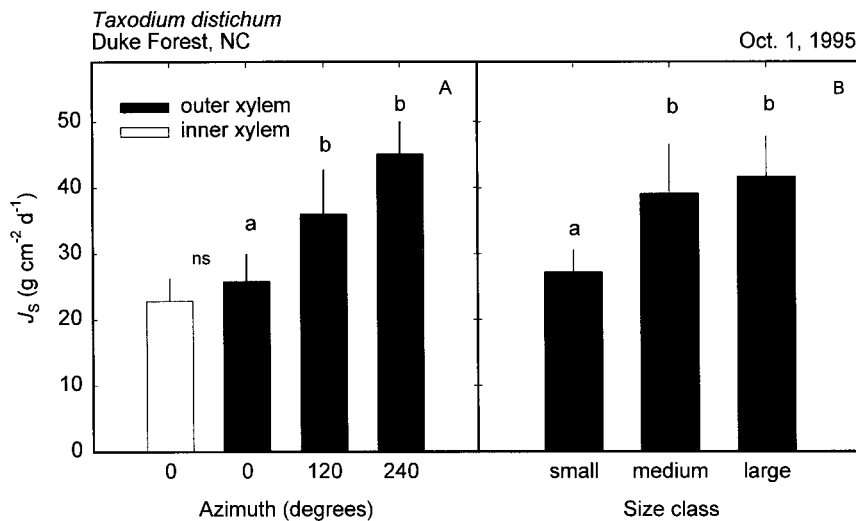


Figure 1. Daily means of sap flux densities (J_S) in (A) three azimuth categories and two depth categories, and (B) three tree size classes. Vertical lines represent ± 1 SE (see Table 1 for values of n).

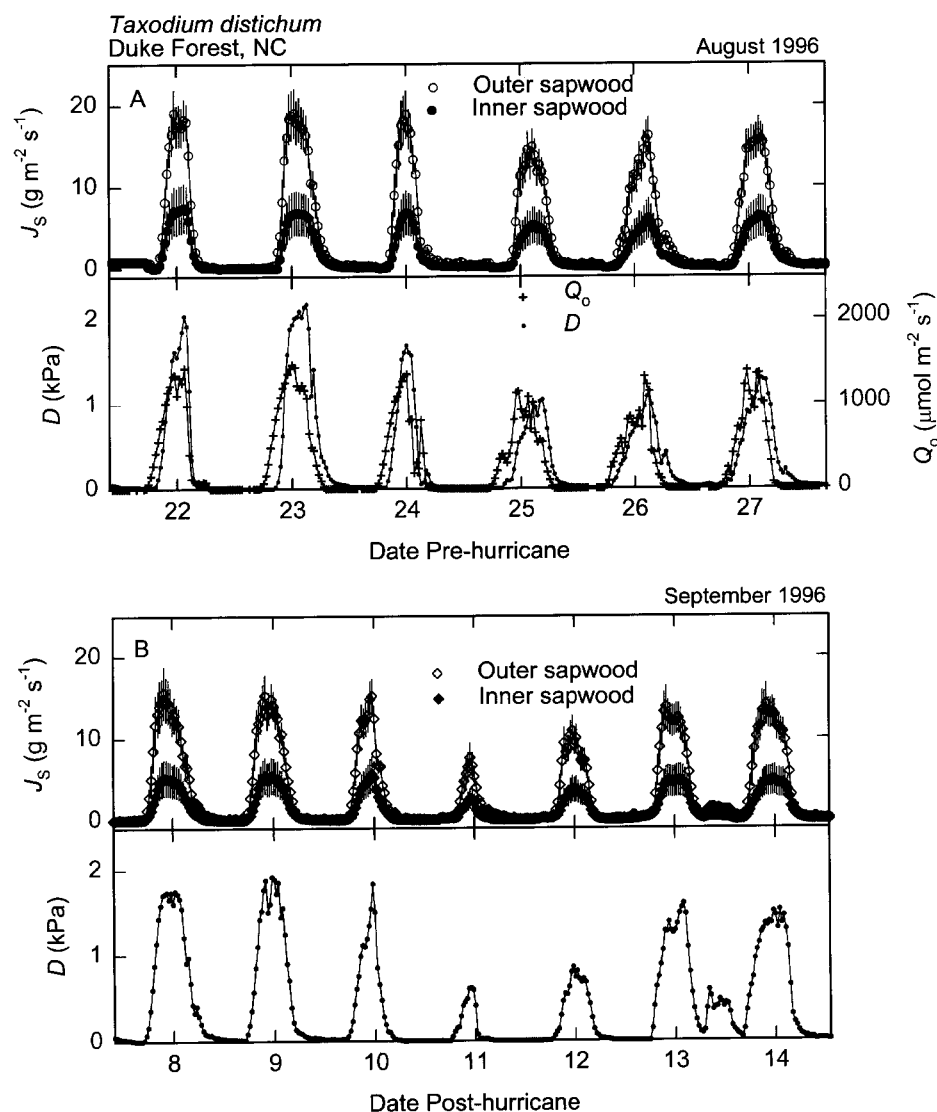


Figure 3. Half-hourly patterns of sap flux density (J_s) in the outer 20 mm and the next (inner) 20 mm of the sapwood, along with vapor pressure deficit (D) and photosynthetically active radiation (Q_o) for the (A) pre-hurricane period, and (B) post-hurricane period, in which Q_o was not measured. Vertical lines represent ± 1 SE ($n = 10$ and 5 for outer and inner sapwood, respectively).

unchanged relationship between J_s and the driving variables, D and Q_o . Because of the misalignment of the light sensor by the storm, only D was available for the post-hurricane period. Despite a similar range in D for both periods, post-hurricane half-hourly patterns of J_s reached a lower maximum than before the hurricane (Figure 3B).

The effect of hurricane Fran on water uptake became apparent when the daily sum of J_s was plotted against mean daytime D normalized by day length/24 h (D_z), to correct for the effect of changing day length on transpiration (Oren et al. 1996). There was a linear relationship between J_s and D_z in both the inner and outer xylem (Figure 4A and 4B; $P < 0.001$ for all regressions), with post-hurricane data sharing the same slope with pre-hurricane data, but shifted lower ($P > 0.15$ and < 0.01 for differences in slopes and intercepts, respectively, for both xylem depths). On average, the shift reflects a post-hurricane:pre-hurricane J_s ratio of about 0.83 and 0.78 in outer and inner J_s , respectively, over the range of D_z values common to both periods. There was no significant departure from linearity

in the relationship ($P > 0.1$). Assuming that J_s reaches zero when D_z does, a second-order polynomial through the origin shows a similar fit to the linear model within the range of the data (P for the second-order term was < 0.002 for all but the pre-hurricane inner xylem for which $P = 0.34$), indicating that the relationship may saturate at high D_z values.

Stand-level transpiration, E_c , was scaled from J_s by weighting J_s measured in 1996 in the inner and outer xylem bands, and multiplying by the plot sapwood area per unit of ground area. The weighting scheme for J_s accounted for differences in flux between northerly and southerly oriented sensors, between inner and outer xylem, and between small and other tree sizes (Table 1). To weight J_s , we used the ratios between (1) sensors positioned toward the north and the mean of sensor pairs positioned toward the south, assuming one third of the sapwood area is represented by the northern sensor (Figure 1A), and (2) small and other tree sizes (Figure 1B); both ratios were calculated from the data collected in 1995, and were used separately for inner and outer J_s . The resulting four

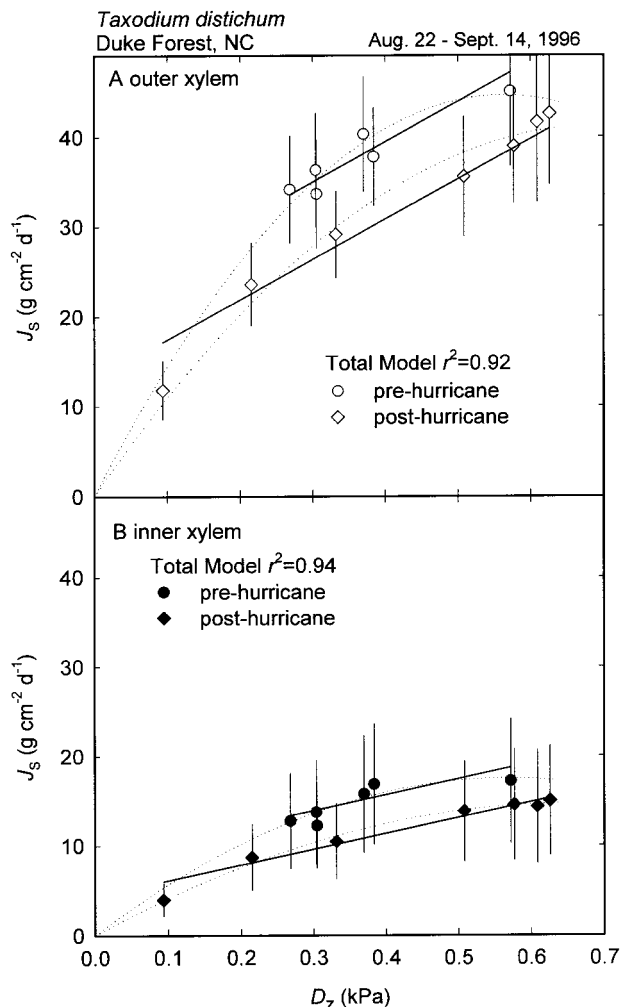


Figure 4. Effects of day-length-normalized daily mean vapor pressure deficit (D_z) on sap flux density (J_s) in (A) the outer 20 mm of the sapwood, and (B) the next (inner) 20 mm of the sapwood in pre- and post-hurricane periods. In each comparison, the slopes are similar but the intercepts are significantly different ($P < 0.01$); vertical bars represent ± 1 SE.

values of weighted J_s (i.e., inner versus outer xylem, small versus other tree sizes) were multiplied by the plot's sapwood area in each category based on the size distribution shown in the inset of Figure 5, and divided by the plot area.

Based on this information, daily E_c (mm day^{-1}) was calculated for the periods before and after the hurricane (Figure 5). Daily E_c reached a pre-hurricane maximum of 1.3 mm day^{-1} . When compared at a similar D_z , post-hurricane E_c was 0.82 of that of pre-hurricane E_c . There was a linear relationship between E_c and D_z ($P < 0.001$ for both regressions), with the post-hurricane data sharing the same slope with the pre-hurricane data, but shifted lower ($P > 0.20$ and < 0.01 for differences in slopes and intercepts, respectively).

At a half-hourly scale, water uptake rate tended to saturate at high D values in both outer and inner xylem, again following a lower trajectory in the post-hurricane period than that in the

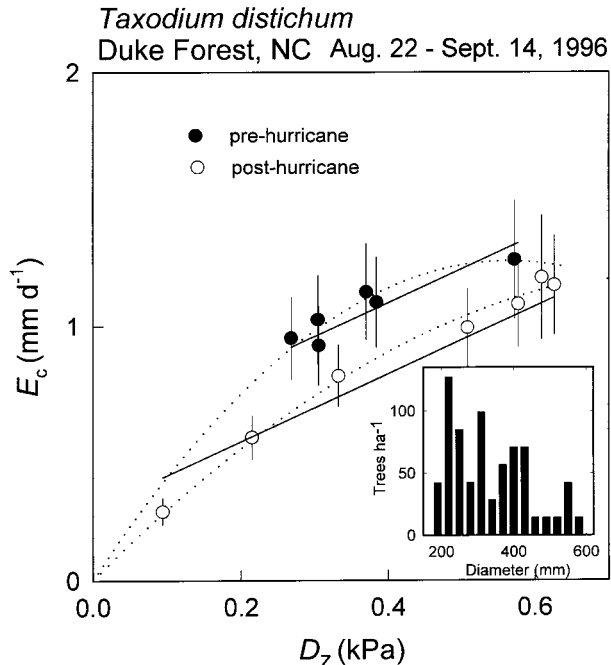


Figure 5. Effects of day-length-normalized daily mean vapor pressure deficit (D_z) on canopy transpiration (E_c) in pre- and post-hurricane periods. The slopes are similar but the intercepts are significantly different ($P < 0.01$); vertical bars represent ± 1 SE. Inset represents the frequency distribution of tree diameters in the stand.

pre-hurricane period (Figure 6). Although the relationship with D did not include a hysteresis commonly seen when a lag occurs between D -driven transpiration and water uptake, an average of a 1-h lag between Q_o and uptake was reflected in the large hysteresis seen for the pre-hurricane period. Thus, with respect to light, uptake begins 0.5–1.5 h after dawn when D begins to increase, and continues into the night, as long as D has not reached zero. Variation among trees in lags between J_s and Q_o were unrelated to tree size ($P > 0.05$). Nighttime flux, mostly in the outer xylem, appeared to accompany a nighttime surge in D on September 13 (Figure 3B).

The half-hourly pattern of canopy transpiration was estimated by weighted mean J_s as calculated above, but weighted again by the sapwood area per unit of ground area of each of the four categories. This value was multiplied by the stand-level $A_s:A_1$ ratio to estimate mean canopy leaf transpiration (E_l , in mmol m^{-2} projected leaf area s^{-1}). Parameter E_l was analyzed in relation to both D and Q_o . Based on stepwise multiple regression, D , D^2 , Q_o , and the interaction $D \times Q_o$ explained 95, 3, 0.03, and 0.004% of the variability in E_l , respectively (all variables were significant at $P < 0.01$; model adjusted $r^2 = 0.98$), but a second-order polynomial model with D explained the variation equally well ($P < 0.0001$; $r^2 = 0.97$). After the hurricane, a second-order polynomial model with D explained nearly as much of the variation in E_l as before the hurricane ($P < 0.0001$; $r^2 = 0.94$), if the nighttime surge in flux was excluded. This nighttime E_l was also highly correlated with D ($P < 0.001$; $r^2 = 0.87$). All three relationships had a zero

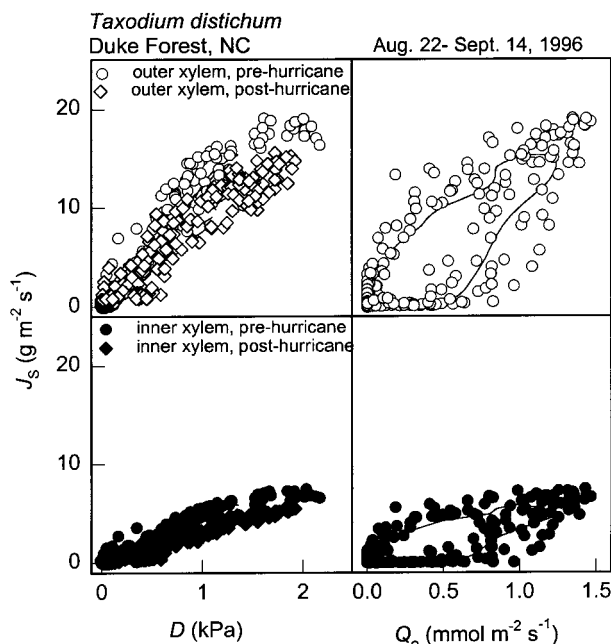


Figure 6. Half-hourly relationships between sap flux density (J_s) and vapor pressure deficit (D) in the pre- and post-hurricane period (left), and photosynthetically active radiation (Q_o ; right) in the pre-hurricane period in the outer 20 mm of the sapwood (top) and the next (inner) 20 mm of the sapwood (bottom).

intercept ($P > 0.1$), and the coefficients for D and D^2 were: 1.23 and -0.27 before the hurricane; 0.84 and -0.10 during daytime after the hurricane; and 0.42 and -0.45 at night after the hurricane.

Discussion

Scaling and estimating E_1

Approaches for scaling stem water flux measurements differ, depending on the type of sensor and the desired uppermost scale, but all approaches are designed to account for systematic variation in stem flux that might occur between the measurement and the uppermost scales (Ěermák 1989, Hatton and Wu 1995, Hinckley et al. 1998, Oren et al. 1998b). Random variation in J_s can be quantified by appropriate replication of J_s measurements within each scaling class (Ěermák et al. 1995, Hatton et al. 1995), and appears to be lower in conifer species than in broadleaf species (Oren et al. 1998b). Random variations in J_s in *Taxodium distichum* were similar to those found in other conifers, as indicated by the number of samples (maximum of 10) required to obtain a CV of 15%.

Scaling J_s to E_1 requires that systematic variation among measured xylem patches is quantified. Radial patterns in J_s have often been investigated (see Phillips et al. 1996), and *T. distichum* shows the commonly observed pattern of a large radial decline in J_s with depth (Figures 1 and 2), indicating that xylem conductivity decreases rapidly with depth. The effect of azimuth was to increase J_s on the southern, more irradiated

side of plants (Figures 1 and 2), which is similar to the findings of several other studies (Daum 1967, Miller et al. 1980, Ěermák et al. 1984, Fichtner and Schulze 1990). In our study, differences in flux among directions indicated that, despite a large distance between sensors and crowns, sensors measured water flux mostly to the crown section directly above.

The effect of tree size is more commonly investigated in relation to total flow than to J_s (see Oren et al. 1998b). Parameters J_s and E_1 of individual trees are not always related to the size of individuals in a stand (Granier et al. 1992). However, in a forest composed mostly of *Nothofagus fusca* (Hook. f.) Ęrst., emergent trees had higher J_s than canopy trees, which, in turn, had slightly higher J_s than sub-canopy trees (Kelliher et al. 1992). This ranking may reflect vertical gradients in microclimate, or an inverse ranking of $A_s:A_1$, which also changes vertically in the canopy (Oren et al. 1986). Decreasing E_1 with tree size in a dense *Abies amabilis* Dougl. ex J. Forbes stand has been attributed to decreasing stomatal conductance because leaf boundary layer conductance and canopy aerodynamic conductance were high, and because small trees were likely to experience very low light (Martin et al. 1997). In our study, the lower J_s in small trees than in medium and large trees may reflect lower irradiance; however, the low LAI of the stand suggests that low irradiance was not the main reason for the difference. Under competitive stress, *T. distichum* produces bands of resin-filled cells (Brown and Montz 1986), such that small trees under intense competition may contain more resin-filled cells per unit of xylem area than unstressed trees. Because these cells would reduce hydraulic conductance, small trees may also have greater $A_s:A_1$ (Whitehead et al. 1984). Without an accurate estimate of $A_s:A_1$ for each tree, we cannot reach a definitive conclusion about the effect of size on J_s .

Sources of variation in daytime E_1 and E_c

Daily E_1 in our study was similar to values reported for a floodplain forest where mean D was higher than during our measurement period (Brown 1981), but daily E_c in our stand was lower because of lower LAI. Daily E_c was correlated to D_z (Figure 5), as were the outer and inner J_s from which it was scaled (Figure 4). Although the best model was linear, a second-order polynomial model described the relationship better based on the distribution of residuals, the ability of the second model to capture the zero intercept, and to saturate at high D_z . Martin et al. (1997) also showed saturation of E_c with increasing daily mean D , but also found that net radiation explained some of the variation in E_c . In our study, the addition of the daily sum of Q_o did not reduce the unexplained variation.

Before analyzing half-hourly responses of E_1 to atmospheric variation, it is necessary to evaluate the potential effect of stored water on the link between J_s and E_1 . In interpreting the relationship between J_s and D , a counter-clockwise hysteresis indicates use of stored water (Doley 1967, Schulze et al. 1985, Meinzer et al. 1997) in proportion to the width of the hysteresis (Hinckley et al. 1978). In our study, the absence of such a hysteresis (Figure 6) serves as a condition for analyzing data at a temporal scale of less than a day. Although this condition cannot be used as a proof that the first assumption is correct, it

provides strong support. Water taken up after sunset was less than a third of that taken up from moist soil by *Pinus taeda* L. trees that were only half as tall (Phillips et al. 1996). Unlike *P. taeda*, which closes stomata at night and uses water uptake for recharge, nighttime water uptake by *T. distichum* is mostly used for transpiration, as indicated by the rapid response of J_s to D at night (Figure 3B). Thus, use and replenishment of water stored in this species is not large, allowing estimation of E_1 from J_s at sub-daily time scales.

Vapor pressure deficit and light explained more than 98% of the variation in half-hourly E_1 during the period before the hurricane, but nearly all of this variation was also explained by a second-order polynomial fit to D alone (Figure 7). Thus, light may exert control over E_1 during a small portion of the daytime hours only. Brown et al. (1984) also found a high response of E_1 to D in mature *T. distichum* trees, but leaves at the bottom of trees transpired over a shorter part of the day, and at lower rates than leaves in the middle and the top of trees, indicating stomatal sensitivity at very low light. Their stands, however, displayed higher LAI than our stand (Brown et al. 1984), and periods of insufficient light may be more restricted in our study stand. Although net assimilation rates of *T. distichum* seedlings reached light saturation at $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Pezeshki and Anderson 1997), seedlings grow equally well from 100 to 25% of full light, in part by adjusting specific leaf area, and maintaining a nearly constant light-saturated net assimilation rate on a leaf-area basis over this wide range of light (Neufeld 1983). The low correlation between Q_o and D in our study provided a clear demonstration of the minor effect of light on canopy conductance, which was probably limited to low light conditions only. Because Q_o and available energy are highly correlated, the response described in Figure 7 indicates that available energy had a minor effect on latent heat flux, and that

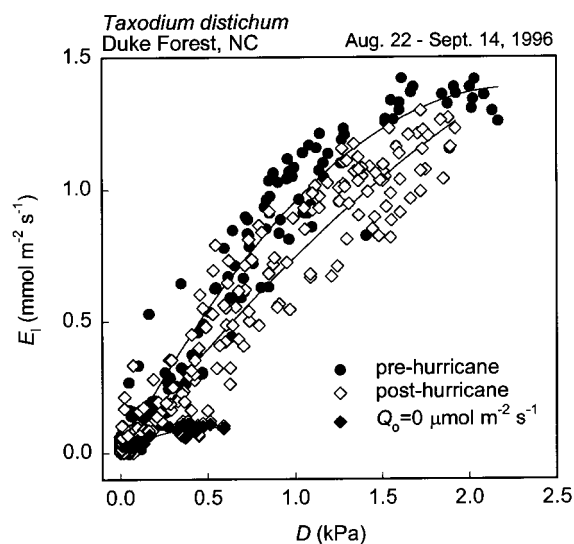


Figure 7. Canopy transpiration per unit of leaf area (E_1) in relation to vapor pressure deficit (D) for the pre-hurricane period, and separately for daytime and nighttime ($Q_o = 0$) in the post-hurricane period. See Results for regression statistics.

the canopy was well-coupled to the atmosphere (Whitehead and Jarvis 1981, Martin 1993). Thus, in *T. distichum* stands of low LAI, the period during daylight hours in which light affects transpiration may be constrained by morphological and physiological adjustments. This is reflected in the strong relationships between E_c and D_z (Figure 5), and E_1 and D (Figure 7).

Sources of variation in nighttime E_1

Nighttime transpiration was evaluated only for the post-hurricane period because D was rarely above zero at nighttime before the hurricane (Figure 3A). Nighttime E_1 increased with D at approximately 50% of the daytime rate, but reached a maximum at $D < 0.5$ kPa (Figure 7, see coefficients in the Results). Nighttime transpiration has been measured in several woody species (Green et al. 1989, Steinberg et al. 1990, Iritz and Lindroth 1994, Hogg and Hurdle 1997). A technical evaluation of a mass flux sensor using a solitary sapling of *T. distichum* showed nighttime transpiration followed the pattern of air temperature, and thus D (Steinberg et al. 1990). In a willow (*Salix viminalis* L.) stand, mean hourly transpiration rates at nighttime were 7% of daytime rates, both because of lower stomatal conductance and lower driving force (Iritz and Lindroth 1994). Compared at similar values of D , nighttime hourly transpiration rates in an aspen (*Populus tremuloides* Michx.) stand were slightly more than 10% of daytime values (Hogg and Hurdle 1997). In the willow stand, E_1 must have increased little with increasing D because of an accompanying increase in canopy resistance, whereas in the aspen stand E_1 increased linearly with D up to values of $D \approx 2.5$ kPa. Thus, the nighttime response of E_1 in *T. distichum* to D was similar to that of the willow, showing a rapid increase in resistance as D increased, but nighttime E_1 of *T. distichum* reached higher proportions of the daytime rates at comparable D than nighttime E_1 of either aspen or willow. Keeping stomata open at night may confer an advantage on hydric and mesic species at times of no soil water limitation because it allows carbon assimilation in early morning to be limited only by the biochemical time constant in response to light.

Effect of leaf area reduction on E_1

Transpiration of trees and stands is related linearly to their leaf area at low leaf areas (Cienciala and Lindroth 1995, Sala et al. 1996), but tends to saturate at high values (Vertessy et al. 1995, Granier and Bréda 1996). In *P. taeda* trees in a nearby stand of comparable LAI to that of our stand of *T. distichum*, increased mean canopy stomatal conductance fully compensated for a 45% reduction in leaf area (Pataki et al. 1998b). We took advantage of an unplanned experimental reduction in LAI caused by hurricane Fran to evaluate the effect of a sudden decrease in leaf area on transpiration. Assuming that trees maintained the same nighttime stomatal conductance after the hurricane as they had before the hurricane when compared at low D (≈ 0.2 kPa), the reduction in nighttime E_c should be proportional to a reduction in LAI. Based on the reduction in nighttime E_c at low D , we estimated that approximately 40% of the leaf area was lost.

The estimated 40% reduction in LAI resulted in reductions of only about 20% in J_s and E_c (Figures 4 and 5), indicating that some stomatal compensation occurred. If our estimate of leaf loss is correct, then *T. distichum*, unlike *P. taeda*, is unable to compensate for reductions in leaf-to-sapwood area by increasing conductance. In *T. distichum*, a reduction in leaf area caused E_1 to increase more slowly with increasing D below 1 kPa, and to approach saturation at higher D (Figure 7; see coefficients in Results) compared with values before the hurricane, indicating that the effect of an increase in $A_s:A_1$ is to reduce water stress at high D , probably allowing the stomata to remain more open than they could at full leaf area. Thus, stomatal compensation for a loss in leaf area involves reduced stomatal sensitivity to D , in addition to increased maximum canopy stomatal conductance associated with decreased light attenuation, and increased supply of water to a smaller leaf area.

Conclusions

Under conditions in which soil–root interface resistance was low and nearly constant, most of the variation in both daytime and nighttime transpiration was explained by variation in D . During nighttime, the increased resistance to transpirational water flow with increasing D at low D values was probably associated with a mechanism unrelated to leaf water potential. During the daytime, the increase in resistance with increasing D at high D values was probably associated with decreasing leaf water potential (Fuchs and Livingston 1996). This interpretation is supported by the finding that both the slope and the curvilinearity of the response of E_1 to D decreased after leaf area was reduced by the hurricane. Lower transpiration rates, which accompany reductions in leaf area, should reduce the rate at which water stress develops during the day at a given D , allowing stomata to remain partially open while maintaining water potentials at a safe margin above critical values (Sperry et al. 1998).

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